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Genetic Study on Milled Rice Amylose Content by Means of Single-Grain Amylose Analysis[1]

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Abstract: Amylose content of milled rice is a significant quality parameter. Genetic analysis of amylose content was conducted using single-grain amylose analysis. Intermediate amylose content to low appeared to be controlled by a single incompletely dominant gene in the combinations between the intermediate and low amylose parents. Two incompletely dominant complementary genes conditioning high over low were suggested from the combinations between high and low amylose parents. A genetic hypothesis of a single incompletely dominant gene controlling high to intermediate amylose was fitted in mating high with intermediate amylose parents. Evidence that amylose content was also influenced by genes of minor effects, or modifiers was also observed in some combinations. The segregation model of endosperm characteristics was illustrated under the assumption of no dosage effect.

Key words: Genetic studies, Milled rice, Amylose content, Single-grain amylose analysis.

INTRODUCTION

Amylose content of milled rice is considered as one of the most important quality parameters for predicting rice eating and processing behavior[13,21,27,28]. However, much of amylose data obtained up to 1971 was traditionally used the method reported by Williams et al[28]. or its modified procedures[12]. These methods for amylose content determination were base upon bulk seed sample with sample size ranging from 100 mg rice flour recommended by Williams et al.[28] to 500 mg used in the studies of Stansel[24]. Due to scientist's endeavors and advances in the precision of analytic instruments, a totally automated procedure for analysis of whole grain of milled rice has been innovated[25].

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Amylose content of the rice grain has been considered as the result of the interaction between genetic properties and environment factors. Amylose content within a rice cultivar could vary by as much as 6 percentage points[1]. Among the different environment factors affecting amylose content, temperature during grain ripening was the dominant factor [2,5,16,22,24], followed by nitrogen fertilization and the degree of milling[20]. Besides, there was some variation between individual rice plants, between panicles within a plant[7,20], and between individual grains within a panicle[26], with a higher variation between panicles than between individual plants. Thus, the use of bulk samples for amylose determination has been recommended[7,20].

Based upon single-grain amylose analysis, Kumar and Khush[15] indicated that the genes for high amylose content were completely dominant to intermediate or low and amylose content was controlled by a single gene or two complementary genes and modifiers, varying from cross to cross. Dosage effects appeared to be observed, depending on the rice entries evaluated[10,14,15]. However, most of published reports, based upon bulk seed analysis, indicated that high amylose content was incompletely dominant to low and was controlled by one major gene and several modifiers[3,18,23]. The role of two complementary genes was indicated in some studies[8,18,24]. The genetic system deduced from the distribution of amylose content in F_2 populations indicating typical quantitative inheritance was shown in another studies [3]. Transgressive segregation for amylose content was found in some studies[3,18], but not observed in another study[24].

In Taiwan, there have been several published genetic reports in relation to milled rice amylose content[4,9,16,17]. However, in these studies, high×low cross combinations were used as experiment materials and bulk seed sample was analyzed for amylose content determination. So far, the genetic analysis of amylose content by means of single-grain amylose determination has not yet been presented in Taiwan. The objectives of thes report were to introduce the method of single-grain amylose determination to the rice scientists of Taiwan and to present some basic genetic information deduced from high×intermediate, intermediate×low, and high×low amylose combinations.

MATERIALS AND METHODS

F_2 combinations evaluated were from the crosses of mating Lemont with Taichung Sen 10 (TCS 10) and Rexmont with TCS 10, as well as Guichow with Lemont. Among these rice entries, Lemont with intermediate amylose content represents a high quality traditional southern U.S. long-grain cultivar and is now a leading cultivar in the southem rice-producing states of USA. TCS 10, a high yielding indica rice cultivar, was released from Taiwan, ROC rice breeding program in 1975 with a high yielding and quality (in particular low amylose level) as priorities. Rexmont with amylose content 2-4% higher than those of the traditional southern U.S. long-grain cultivars was developed specifically to satisfy the rice industry's need. Guichow, an indica short-grain cultivar with high amylose content, was released from China mainland under a breeding program with high yielding as a priority.

The detailed mating scheme was referred to as listed in Table 1.

Amylose content of a whole milled rice grain was determined by following the method innovated by Webb[25] using a Technicon AutoAnalyser (Technicon Instruments Corp., Tarrytown, NY). The detailed procedures are: on Day 1, a single kernel is weighed and placed into a 25mm×100mm test tube, and then is soaked overnight in a 2ml 1.7% KOH. On Day 2, 1 ml 2.5N NaOH is added and then agitated vigorously with a Vortex shaker. On Day 3, a single grain sample placed in the test tube is tissumized 30 seconds with a tissumizer at 45-50 rpm and the blade of tissumizer on shaft is rinsed with 17ml distilled water. The sample is then shaken vigorously again with a shaker. On Day 4, The single grain samples are shaken again before starting a run with a Technicon AutoAnalyser. The data obtained are corrected by the grain weight that had been recorded on Day 1.

RESULTS

Mating Lemont with TCS 10

The mean amylose content of the intermediate amylose parent, Lemont, was 23.2% (a total of 40 random milled rice grains) with a range from 21 to 25% and a mode at 23%. The low amylose parent, TCS 10, had a mean of 15% (40 grains) with a range from 12 to 17% and a mode at 15%. A difference in amylose content between the two parents was approximately 8%. The coefficients of variation of the two parents were 4.81% for Lemont and 10.63% for TCS 10, respectively. It is well known that the coefficients of variation of the parents are regarded as an estimate of the environment variation under the condition of the test. Thus, it appeared, form the data mentioned, that environment effect on differentiating amylose content between two parents, Lemont and TCS 10, seemed different slightly. However, the frequency distributions of milled rice amylose content for the parents were similar, and both showed approximately normal distributions (Fig. 1).

The 360 F_2 seeds of the Lemont x TCS 10 combination ranged in amylose content from 12 to 29% with a mean of 22.3% and a coefficient of variation of 19.12%. In contrast, in the F_2 seed population of TCS x Lemont combination had a mean amylose content 22.4% with a range from 12 to 30% and a coefficient of variation of 19.79%. It is well recognized that the coefficient of variation of the F_2 population is a measurement of the total variation, i. e., both environment and genetic variation. In the present case, one could suppose that both environment and genetic variation involved in these two F_2 populations were approximately similar.

The frequency distributions of milled rice amylose content of F_2 seed populations in both combinations exhibited continuous but appeared to be bimodal curves (Fig. 1). Maximum frequency classes were observed at 16 and 23% in Lemont x TCS 10 combination and 16 and 24% in TCS x Lemont combination, respectively. On the other hand, minimum frequency classes were found at 20% in both combinations. According to Juliano[11], amylose content of milled rice is traditionally classified as low (below 20%), intermediate (20-25%), and high (above 25%). Thus, the distributions of two F_2 seed populations could be

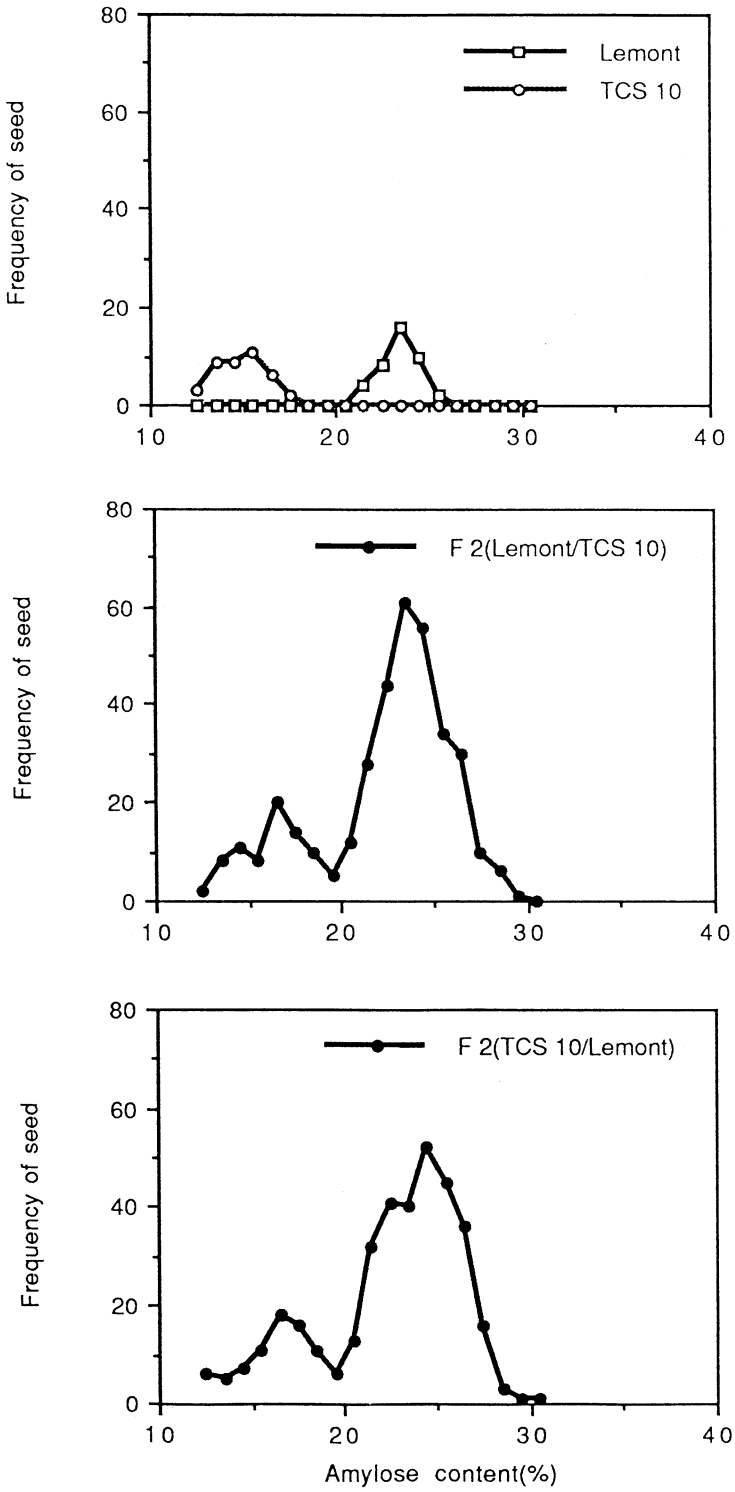

Fig. 1. Frequency curve showing distributions of amylose content in the combinations between Lemont and TCS 10.

categorized into two amylose groups: a low amylose group and an intermediate amylose group with approximately one-fourth of the seeds falling into low groups (78 in Lemont x TCS 10 and 80 in TCS 10 x Lemont combinations, respectively) and three-fourths in the intermediate groups (282 in Lemont x TCS 10 combination and 280 in TCS 10 x Lemont combination, respectively), suggesting segregation of one pair of major genes, with intermediate amylose incompletely dominant. The hypothesis of a single major gene conditioning amylose content in these combinations was further tested. The Chi-square (X^2) values indicated a very good fit to a 3 intermediate: 1 low segregation ratio (Table 1).

Table 1. Chi-square values for test of goodness of fit to genetic segregation models for amylose content of the rice combinations studied.

Combination[z]	Number of F_2 seed	Genetic model	Expected segregation	df	X^2	P
Lemont/TCS 10	360	1 dominant gene	3 : 1	1	2.13	0.20-0.10
TCS 10/Lemont	360	1 dominant gene	3 : 1	1	1.48	0.30-0.20
Rexmont/TCS 10	360	2 complementary genes	13 : 3	1	0.37	0.80-0.70
TCS 10/Rexmont	360	2 complementary genes	13 : 3	1	0.04	0.90-0.80
Guichow/Lemont	180	1 dominant gene	3 : 1	1	2.40	0.20-0.10
F_1/Guichow	100	1 dominant gene	7 : 1	1	0.02	0.90-0.80
F_1/Lemont	100	1 dominant gene	3 : 5	1	1.80	0.70-0.60

[z] In all combinations, the first parent indicates the female parent and the second male.

A larger number of transgressive segregates for high amylose content were observed in both F_2 populations. These would indicated that the low amylose parent, TCS 10, carried, in addition to a pair of genes of major effect for low amylose content, certain modifiers of minor effect for high amylose content[3,4,6]. Therefore, a genetic system of differentiating amylose content in relation to mate Lemont with TCS 10 was controlled by one pair of genes of major effect and modifiers of minor effect, and the major gene for intermediate amylose content was incompletely dominant to its allele.

Mating Rexmont with TCS 10

The mean amylose content of the high amylose parent, Rexmont, was 28.1% (40 grains) with a range from 26 to 29% and a mode at 27%. The mean for the low parent, TCS10 was 15.1% (40 grains) showing a range from 12 to 16% and a mode at 14%. Thus, the parent difference in amylose content was about 13%. The coefficients of variation of the parents were 2.10% for Rexmont and 4.90% for TCS 10, respectively. This indicated that the coefficient of variation of Rexmont was about half that of TCS 10. The frequency distributions of amylose content for the parents seemed to be appeared as skewed rectangles and to be differed from a normal distribution as shown in (Fig. 2).

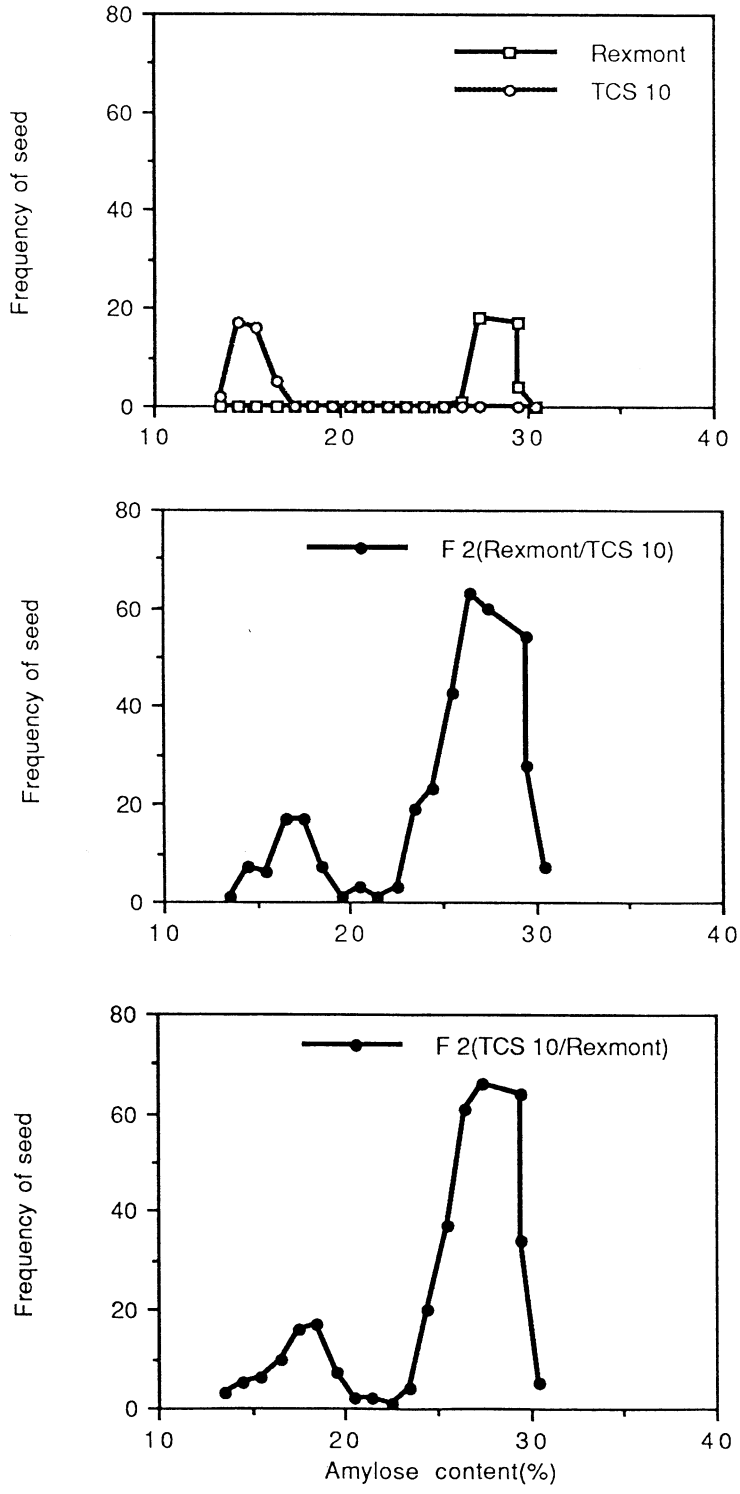

Fig. 2. Frequency curve showing distributions of amylose content in the combinations between Rexmont and TCS 10.

The 360 F_2 seeds in the Rexmont x TCS 10 combination ranged in amylose content from 13 to 30% with a mean 25.2% and a coefficient of variation of 16.19% and that in the TCS 10 x Rexmont combination showed an average amylose content of 25.4% with a range from 13 to 30% and a coefficient of variation of 16.34%, indicating that both environment and genetic variation in these two combinations seemed approximately similar.

The frequency distributions of amylose content of the F_2 seed populations in both combinations formed essentially bimodal curves (Fig. 2). Maximum frequency classes were observed at 17 and 26% in Rexmont x TCS 10 combination and 18 and 27% in TCS X Rexmont combination, respectively. Minimum frequency classes occurred at 21% in Rexmont x TCS 10 combination and 22% in TCS 10 x Rexmont combination, respectively. The F_2 frequency distribution of amylose content in both combinations could be classified into two amylose groups: a low group with approximately three-sixteenths of the seeds (63 in Rexmont x TCS 10 combination and 69 in TCS 10 x Rexmont combination, respectively) and a high group with thirteen-sixteenths of the seeds (297 in Rexmont x TCS 10 combination and 291 in TCS 10 x Rexmont combination, respectively). The results suggested segregation for two complementary major genes, with high amylose incompletely dominant to low amylose. The genetic hypothesis of two complementary genes conditioning high amylose content, which would segregate 13 High: 3 low in F_2 populations, was then tested. The Chi -square (X^2) values supported a satisfactory fit to the 13 high: 3 low complementary gene model (Table 1). That is, a dominant and recessive epistasis was involved in conditioning high amylose in both F_2 populations, i. e., A epistasis to B, b; bb epistasis to A, a. Thus, A- and bb exhibited identical phenotype assuming A and B were incompletely dominant in conditioning high amylose.

Transgressive segregation for amylose content were not observed in these two F_2 populations.

Mating Guichow with Lemont

The mean amylose content of the high amylose parent, Guichow, was 27.5% (20 random milled rice grains) with a range from 25 to 28% and a mode at 27%. The mean of the intermediate amylose parent, Lemont, was 23.6% (20 grains) having a range from 22 to 24 %and a mode at 23%. Therefore, the difference between the parents about amylose content was approximately 4%. The coefficients of variation of the parents were 2.04% for Guichow and 2.54% for Lemont, respectively. It is simply because the coefficients of variation of the parents are usually regarded as an estimate of the environment variation under the condition of the test. Thus, the environment effects on amylose content for the parents, Guichow and Lemont, appeared approximately similar. Besides, the frequency distribution of amylose content for the parents showed typically normal distributions (Fig. 3).

The 180 F_2 seeds of the Guichow x Lemont combination ranged in amylose content from 21 to 30% with a coefficient of variation of 7.51% and a mean of 26.9%, which was about1.5 % higher than that of the mid-parent 25.5%. The 100 F_2 seeds of F_1 x Guichow combination had a mean amylose content of 27.2% with a range from 21 to 30% and a coefficient of

variation of 6.62%. The 100 F_2 seeds of F_1 x Lemont combination showed an average amylose content of 25.2% with a range from 21 to 29% and a coefficient of variation of 7.38%. These figures suggested that a slight differences in the total variation for amylose content might exist among the three F_2 seed populations. It is well recognizes that the coefficient of variation for the F_2 population is a measurement of both genetic and environment variation. Thus, the slight difference in total variation in the three populations were probably due to genetic variation because that environment effects on amylose content for the parents seemed approximately similar under the condition of the test, i. e., environment effects in the three populations on influencing amylose content, thus, could be considered to be similar.

The frequency distribution of the F_2 seed amylose content in the Guichow x lemont combination was continuous but appeared to be bimodal, with maximum frequency classes at 24 and 28% and minimum frequency class at 25% (Fig. 3). The distribution of the F_2 seed population could be divided into two groups: a high amylose group and an intermediate amylose group, with approximately one-fourth (36 grains) of the seeds falling into the intermediate group and three-fourths (144 grainls) in the high, indicating segregation for one major gene in conditioning high amylose content and incompletely dominant. When testing genetic hypothesie of a single gene pair conditioning high amylose content was done, Chi-square (X^2) value indicated a good fit to a 3 high : 1 intermediate segregation ratio (Table 1).

The frequency distribution of F_2 seed amylose content in F_1 x Guichow combination formed a skewed curve, with the maximum frequency class at 28%. However, as a genetic hypothesis of a single gene pair conditioning high amylose content was postulated, the F_2 population could be categorized into two amylose groups: an intemediate and a high groups, with approximately one-eighth of the seeds falling into the intermediate group (13 grains) and seven-eighths in the high group (87 grains) as dividing at the class 25%, indicating segregation for one major gene pair conditioning high amylose content but being incompletely dominant. When the genetic hypothesis of a single gene was tested, Chi-square (X^2) value indicated a very good fit to a 7 high: 1 intermediate segregation ratio (Table 1).

The F_2 frequency distribution of amylose content in the F_1 x Lemont combination showed a continuous curve but it seemed bimodal (Fig. 3). The genetic hypothesis for the population was also a single gene conditioning high amylose content. Thus, the frequency distribution of the population could also be categorized into two groups: an intermediate amylose group and a high amylose group, with about five-eighths of the seeds falling into the intemediate group (56 grains) and three-eighths in the high group (44 grains), indicating segregation for one major gene with high amylose content incompletely dominant. The Chi-square (X^2) value demonstrated a very good fit to a 3 high: 5 intermediate segregation ratio (Table 1).

There were many F_2 seeds with high amylose content distributed beyond the range of the high amylose parent, Guichow, in the three populations, suggesting that transgressive

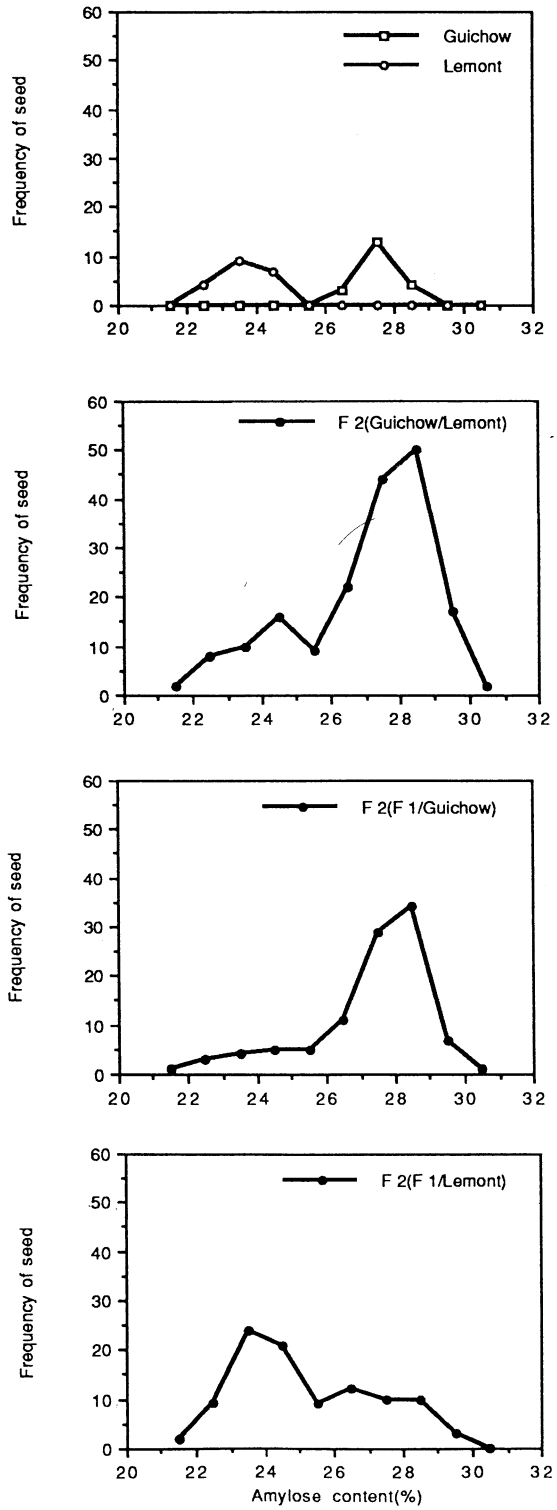

Fig. 3. Frequency curve showing distributions of amylose content in the combinations between Guichow and Lemont.

segregation for high amylose content existed in the populations. This would indicated that the intermediate amylose parent, Lemont, possessed, in addition to a gene pair of major effect for intermediate amylose content and modifiers of minor effect for high amylose content.

DISCUSSION

It is well recognized that an endosperm (grain) is developed from the fusion of two polar nuclei from the female and one sperm nucleus from the male and the occurrence of the fertilized egg is the beginning of a new generation. As the result, the endosperm on a plant represents the next generation, genetic expression for endosperm charzcteristics is under triploid genetic control, and an individual is a grain, not a plant, especifically for concerning the genetic analysis of endosperm characteristics. Because milled rice amylose content, a chemical property of rice starch, is usually considered to be one of the most important attributes for predicting eating, and prosessing quality parameters[13,21,27,28], both traditional bulk seed and single-grain analyses were used to collect the amylose data for the genetic analysis in various rice breding programs. However, so far, many of published genetic studies on amylose content of rice endosperm were traditionally based upon bulk seed analysis of genetically heterozygous plants, i. e., amylose data of F_2 plants were determined by the bulk F_3 endosperm on the F_2 plants, for example.

The detailed genetic information obtained by both amylose determination methods appeared different slightly. Generally speaking, the genetic system deduced from the analysis of bulk seed sample basis indicated that genes conditioning high to intermediate or low or intermediate to low were incompletely dominant. In contrast, Kumar and Khush[15] found that based upon single−grain analysis, genes for high amylose were completely dominant over those for intermediate or low. They argued that analyses of the bulk seed samples of genetically heterozygous plants provided biased information on the inheritance of milled rice amylose content. In their study, when high amylose level parents were mated with low amylose content parents, the frequency distributions of amylose content, based on single-grain basis, for F_2 and F_1 backcrossed to low amylose parent populations showed discontinuous but bimodal curves. Therefore, the genetic hypothesis of a completely dominant gene conditioning high amylose content over low or intemediate amylose level was demonstrated. According to Kumar and Khush[15], the differences in the genetic deductions between most of the published reports and their results is probably due to the bulk seed analysis used in segergating generation (i.e., genetically heterozygous plants) in these genetic studies. In other words, because of segregation for high and low amylose content, bulk seed analysis would give lower values for amylose content in milled rice within each plant. Consequently, complete dominance would appear to be partial or incomplete dominance. However, published data showed that a wide range in values among individual grains on single panicles was observed for various quality characteristics. For example, percent amylose content, based on single-grain basis, of Lemont rice varied from 18 to 27% from which a normal distribution was formed. The mean of thses grains was 22.3%, which was equal to

that of the mean value from bulk sample determinations for amylose content[26]. Also, there is some variation between individual rice plants and between panicles within plants[20]. Thus, data on amylose content collected by Kumar and Khush[15], based on single-grain basis, were undoubtedly confounded by the variation between grains within panicles and between panicles within plants as well as between plants. It is apparent that these differences in the genetic deductions between most of the genetic reports and the report of Kumar and Khush[15] might not be completely explained by the different basis by which the amylose content has been determined. The genetic background of the materials used in an experiment may have also result in different genetic deduction. Thus, the differences in these two genetic deductions could result partially from sample determination basis, i. e., buld seed versus single-grain, and partly from materials having different genetic background.

A genetic hypothesis based on diploid genetic control due to triploid nature of the endosperm is adequate to describe the data of amylose content analyzed by single grain basis as presented in this paper. For example, for a F_1 plant with a Aa genotype for an endosperm characteristic, the probability of possible combinations of polar nuclei in ovule of the plant will be 1 AA: 1 aa and the possible genotypes of the pollens will be 1 A: 1 a. Thus, the possible genotypes of the F_2 seed population will be 1 AAA: 1 AAa: 1 Aaa: 1 aaa. Suppose genotypes of AAA, AAa, and Aaa possess the same phenotype, i. e., no dosage effect, a 3 A--: 1 aaa segrgation ratio will be observed. When a backcross is made between the F_1 and the dominant parent (P1), the possible genotypes will be 1 AA: 1 Aa for the B_1F_1 plants, and 1 AAA: 1 Aaa for the B_1F_1 endosperms. The possible genotypes of the B_1F_1 endosperms will be 1 AAA: 1 (1 AAA: 1 AAa: 1 Aaa: 1 aaa),i.e., 5 AAA: 1 AAa: 1 Aaa: 1 aaa, as the B_1F_1 plants are selfing. Thus, a 7 A--:1 aaa segregation ratio is found. On the other hand, when the F_1 is backcrossed to the recessive parent (P2), the possible genotypes will be 1 Aa: 1 aa for the B_2F_1 plants and 1 AAa: 1 aaa for the B_2F_1 endosperms. The possible genotypes of the B_2F_2 endosperms will be 1 (1 AAA: 1 AAa: 1 Aaa: 1 aaa) : 1 aaa, i.e., 1 AAA: 1 AAa: 1 Aaa: 5 aaa, as the B_2F_1 plants are selfing. Thus, a 3 A--: 5 aaa segregation ratio will be presented. These ratios are then consistent with that of a diploid segregation. Thus, a diploid genetic model in convenience was used to interpret the inheritance of amylose content based on single-grain analysis as presented in this paper. Results obtined showed good fit to the hypotheses made for three amylose content groups studied. Actually, up to now, all published reports, either based on bulk sample determination or by single-grain analysis, all of the genetic deductions were all based on diploid genetic principles even though it is well recognized that genetic expression of endosperm characteristics is under triploid genetic control. However, in this case, dosage effect has to be ignored.

Finally, compared with other plant quantitative characteristics such as plant height, panicle length, etc., a satisfactory quantitative genetic model for endosperm characteristics has not yet been developed although much attention has recently been devoted to the grain quality. The lack of proper genetic models has been an obstacle in studying the inheritance of endosperm characteristics[19]. Therefore, establishing a quantitative genetic models for endosperm characteristics will be of benefit to breeding programs in cereal crops of which

high grain quality is a priority.

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經藉單粒直鏈澱粉分析的白米直鏈澱粉含量之遺傳研究[1]

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摘 要

白米直鏈澱粉含量是一個重要的品質介量，本研究以單粒直鏈澱粉分析進行白米直鏈澱粉含量之遺傳研究。在中與低直鏈澱粉含量親本之雜交組合中，中直鏈澱粉含量對低含量受一對不完全顯性基因所支配。而在高與低直鏈澱粉含量親本的雜交組合中，指出高含量對低含量受兩對不完全顯性的互補基因所控制。一個高直鏈澱粉含量對中含量係受一對不完全顯性基因所支配的遺傳假說則符合高與中直鏈澱粉含量親本的雜效組合。另，直鏈澱粉含量尚受微效修飾基因影響之證據也在本研究一些組合中被發現。文中曾就無基因劑量效應的前提下，例釋胚乳性狀的分離模式。

關鍵詞：單粒直鏈澱粉分析、白米、直鏈澱粉含量、遺傳研究。

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